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BIOLOGICAL RELATIONS OF CERTAIN CACTI¹

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ESPECIAL interest is attached to the study of the cactus family because it is peculiarly well adapted by habit and by structure to withstand the trying conditions of the desert. The greatest development of the group occurs in the arid portions of tropical and subtropical America, but the conception which this statement is likely to give that the cacti thrive best with a modicum of water and live in localities that are too severe for all other desert plants to endure, is erroneous. The cacti like other plants of the desert are most vigorous when the water supply is adequate, and it is by no means certain that such a form as the giant cactus (*Cereus giganteus*) or the barrel cactus (*Echinocactus wislizeni*), as well as the larger *Opuntias*, do not require a larger amount of water than many of the large plants of other families.

However, it is also likely that no desert plants can live and perpetuate their kind under more arid conditions than some of the cacti. The general means by which they accomplish this are too well known to require repetition here, but certain adaptations to desert conditions, not so well known perhaps, may be pointed out. The most important factor in the life relations of the desert plants is unquestionably the available water supply, and the most striking adaptations accordingly are associated with the absorption, the storage, or the conservation of water. This relation to the water supply, either in apparent independence of it or in intimate association with it, is met at each stage of development. For instance, the seeds of the giant cactus will germinate in summer while lying on the top of air-dry sand and without previous wetting. Seedlings of *Opuntia versicolor* are provided with water-storage organs (Fig. 1) although such are absent in the adult plants. The reaction of the mature plants to a variable water supply is also noteworthy. Specimens of

¹ Papers from the Desert Botanical Laboratory of the Carnegie Institution, No. 11.

Opuntia engelmanni, wrinkled from the loss of water during a long drought (Fig. 2), absorbed sufficient water within two days following a storm to make their joints plump and smooth (Fig. 3). The giant cactus is especially adapted by the peculiar for-

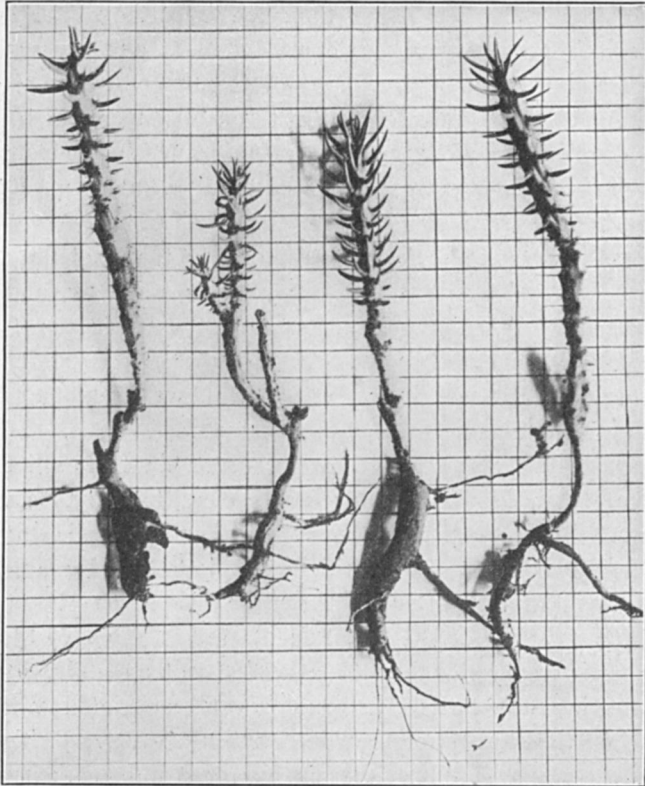


FIG. 1.— Young plants of *Opuntia versicolor* showing the water-storage organs — the swollen roots — which are not present as such in the mature form.

mation of the rind to undergo without injury considerable changes in volume which are induced by a variation in the water content (E. S. Spalding, :05). Other adaptations, such as certain characteristics of the root systems, certain peculiarities of structure and their relation to transpiration, and the transpiration under different conditions may be presented somewhat more fully.



FIG. 2.—*Opuntia engelmannii*, May 11. May 11 marked the close of a severe dry period and the wrinkled surface of the cactus shows that it was suffering from the drought.

THE ROOT SYSTEMS

A special study of the structure and extension of the root systems of desert plants cannot fail to be of great interest and importance in contributing to a right understanding of the biology of these plants. Many characteristics of the desert vegetation are without much question directly traceable to peculiarities of the various root systems. It has been observed (Coville, '93, p. 43) that the fairly equal spacing of desert shrubs is one of the characteristics of their distribution. The primary cause for this is presumably the struggle for water and their distribution is, therefore, an expression of the mutual relationship of the root systems. Again, frequently the form of the root is incompatible with certain habitats,—for example a subirrigated plant would find difficulty in growing where the subsoil is the rock-like *calliche*,—and plants with such deeply penetrating roots, for instance, are for this reason limited in their distribution. It is theoretically possible, and so far as I have observed actually true, that those plants that have a root system which is at once superficial and which penetrates the ground deeply, all other things being equal, may also have the widest choice of habitats. Certain it is that the creosote bush, for example, which has a root system of this character (V. M. Spalding, :04) is perhaps the most widely distributed of our desert shrubs. Although this view of the relation of the character of the root systems to the distribution of these plants is advanced tentatively only, the importance of it as a factor which must be taken into consideration in this connection and sometime carefully studied, is very apparent.

The root system of a specimen of *Echinocactus wislizeni* which was 60 cm. high and 35 cm. in diameter, growing about 75 meters north of the laboratory, was carefully exposed and the course of its roots mapped (Fig. 4). The roots, as the figure indicates, were branched very freely. There were three main roots which arose from the base of the plant not far from 10 cm. from the surface of the ground and which so directed their growth, and that of the branches, that the area compassed by them was about equally apportioned and well covered. As a rule the roots were

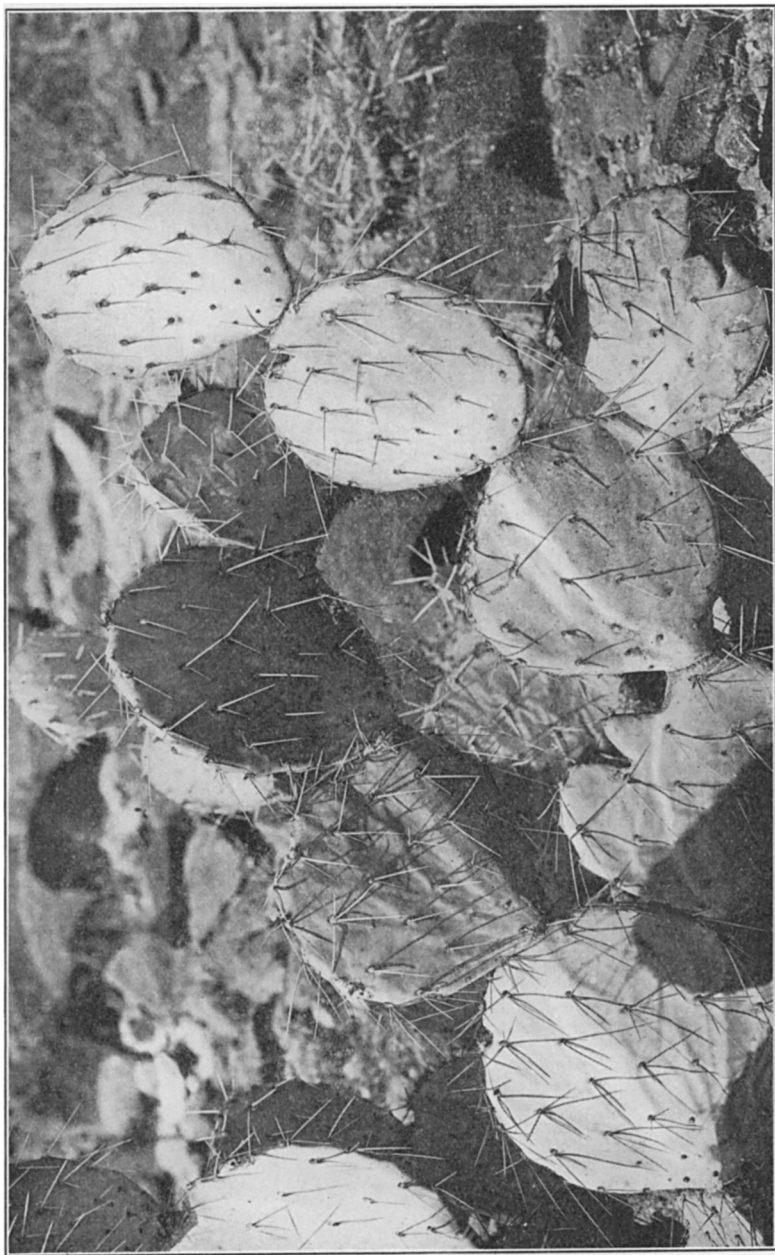


FIG. 3.—*Opuntia engelmannii*, May 14. This is the plant shown in Fig. 2. Rains came May 10-12; the plump condition of the joints of the plant on May 14 indicates that water was absorbed promptly after the rains, and in considerable quantity.

slender. At a distance of 15 cm. from the plant one of the largest of them was 7.6 mm. in diameter, and one meter from the plant it was 4.6 mm. in diameter. The roots ran about 6 cm. below the surface, in places which were free of stones, but when a stone was encountered the root dipped beneath it and availed itself of

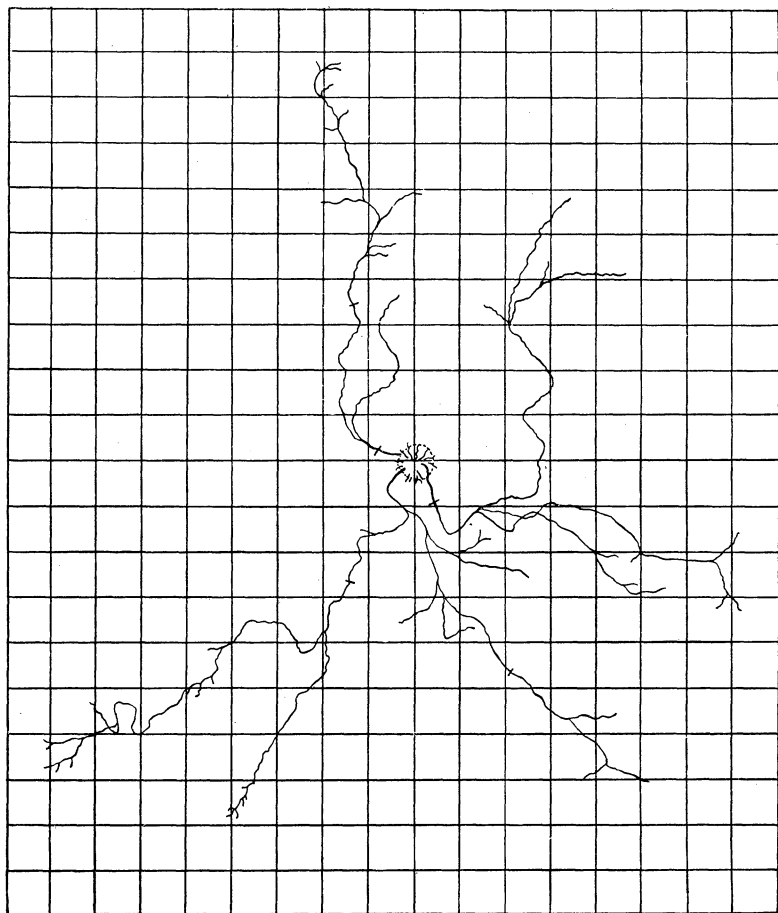


FIG. 4.— Root system of *Echinocactus wislizeni*. Scale: 1 unit = 30 cm.

the better water supply to be found there. The most deeply placed root, however, was not more than 10 cm. below the surface of the ground. There are therefore two noticeable characteristics of the root system of *Echinocactus wislizeni*, namely, the roots

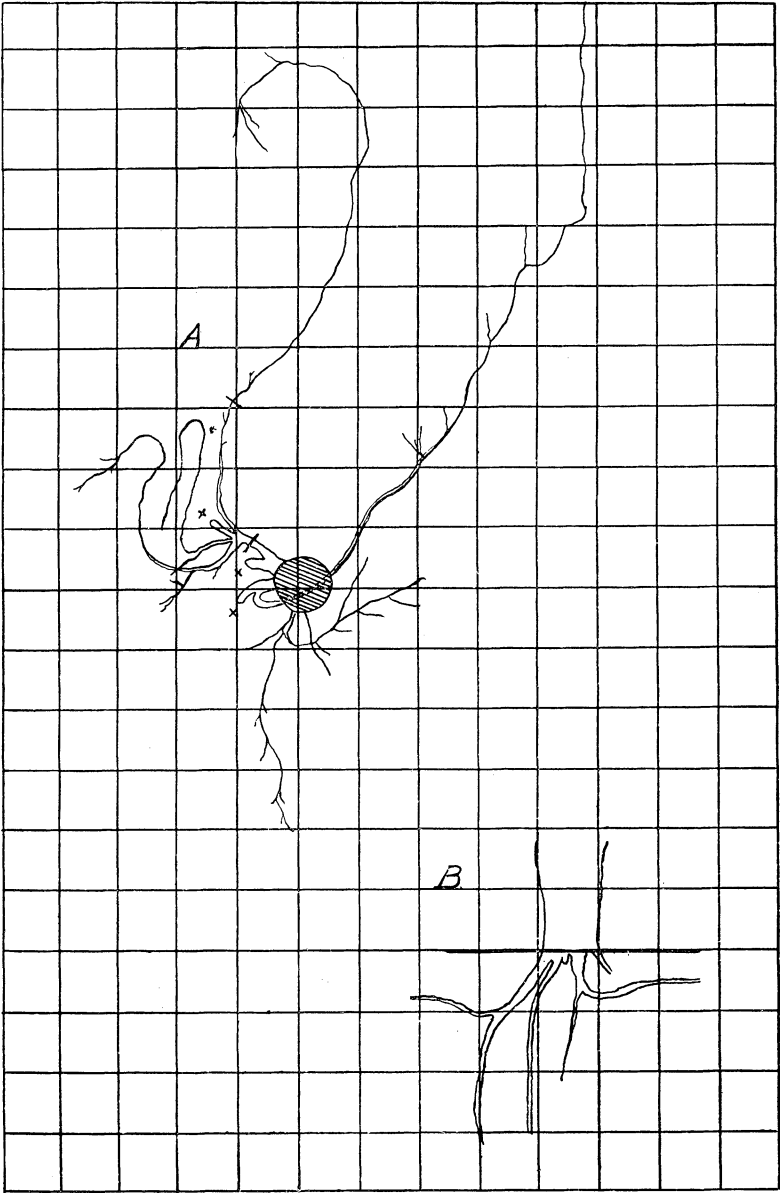


FIG. 5.— Root system of *Cereus giganteus*. Scale: 1 unit = 10 cm.

are slender throughout their entire course and they are superficially placed.

The roots of *Cereus giganteus*, on the other hand, in form and position, and perhaps in extent and branching also, are very different from those of *Echinocactus*. Fig. 5 represents the root system of a *Cereus giganteus*, about one meter high, which was growing 200 meters west of the *Echinocactus* just described. Four main roots were observed to arise from the base of the plant. At first they were relatively heavy, from 2 to 4 cm. in diameter at the proximal ends, but they became smaller very rapidly as the distance from the plant increased—in a manner much as is indicated by *A* of the figure. Very soon after leaving the plant the roots branched. One branch, whose later history could not be traced, struck directly downwards, and the other took a more or less horizontal course. The latter branched at intervals, although perhaps not so frequently as those of *Echinocactus*, and extended, in one instance at least, over one meter from the plant's base. How much farther the root reached could not be learned because of its fragility and the small size of the distal branches. The superficial portion of the root system of *Cereus giganteus* was more deeply placed than were the roots of *Echinocactus*, and owing to the fact that these parts were not so richly branched, the ground included by them was not so thoroughly covered. However, in one characteristic, which is of interest to note but whose significance I have not investigated, the superficial roots of the two forms are alike, namely, the longer roots and the greatest number of roots are situated on the uphill side of the respective plants. This peculiarity is shown in the two figures. In Fig. 4 the uphill side is to the right, and in Fig. 5 it is at the top of the sketch.

CERTAIN STRUCTURAL FEATURES

Perhaps the correlation of structure and function is nowhere more patent than in the peculiar transpiration-controlling and transpiration-promoting tissues, and the rate of transpiration in certain cacti. As is well known, the cacti are well adapted structurally, laying aside for the moment the matter of water storage,

to retain water for long periods. As an illustration of how long a specimen of *Cereus giganteus* must ordinarily retain water in this locality, the following may be suggested. Calculations based upon the known average water content of these cacti, on the estimated spread of the root system, and on the average rainfall at this place indicate that approximately two years' rainfall, assuming the rainfall to be normal each year, 11.74 in., are required to supply a cactus 15 feet high with an amount of water equal to what it usually contains. The necessity of husbanding

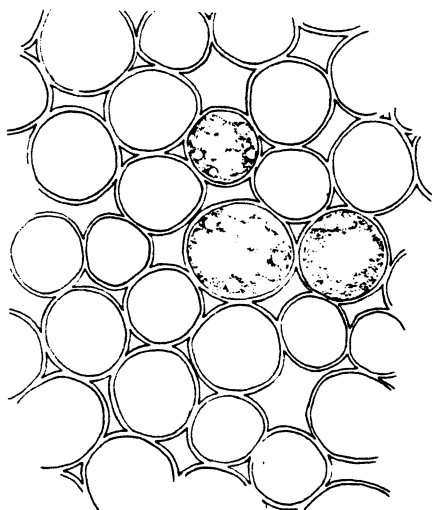


FIG. 6.—*Echinocactus wislizeni*. A portion of the cortex showing chlorenchyma with large intercellular spaces. The section was made parallel to the surface.

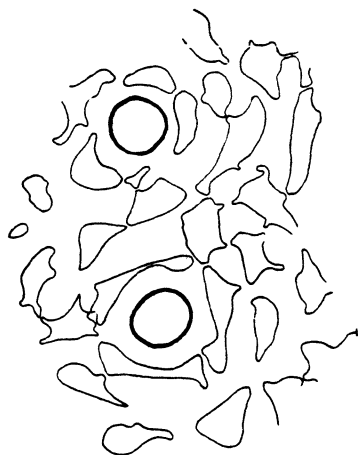


FIG. 7.—*Echinocactus wislizeni*. The heavy-walled supporting tissue lying immediately under the epidermis. This section was parallel to the surface.

the water so hard-gained is even more apparent when the relation of the normal rainfall to the usual evaporation is taken into account. As has been pointed out (Coville and MacDougal, '03, p. 27) the annual evaporation is 7.7 times the rainfall. This is the normal ratio, but when the precipitation is below average, as in 1904 (when it was 75 percent normal) the disparity is even greater (Canon, '05b).

Although, as mentioned above, the structural adaptations for the retention of water are well known, reference should here be made to the special adaptations found in *Echinocactus wislizeni*, par-

ticularly on account of the small rate of transpiration which was demonstrated in this plant. *Echinocactus* has a heavy outer

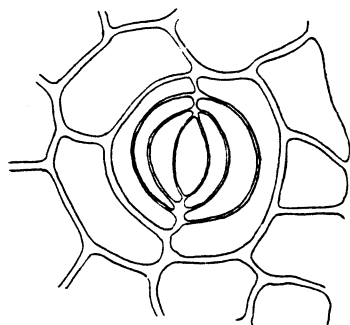


FIG. 8.—*Echinocactus wislizeni*. Surface view of stoma.

membrane which is cuticularized (Figs. 9, 10). The stomata are peculiarly fitted to guard well a too rapid loss of water, and they have a somewhat complicated structure. The stoma as characteristic of many xerophytic plants, is sunken below the general surface of the stem, and from it in *Echinocactus* a tube, divisible into two portions of separate function, leads deeply into the outer portion of the cortex and becomes

the peripheral portion of the extensive intercellular aërating system of the plant. The substomal tube, really trachea, is shown schematically in Fig. 11. The outer portion, which is heavily shaded in the sketch, is cuticularized throughout its course in the sclerenchymatous tissue (Fig. 10) of the cortex, and in this part it acts merely as a tube for the conduction of gases. Beneath the supporting tissue the tube enters the chlorenchyma and its wall is no longer cuticularized; it here functions as the substomal chamber proper.

It is of interest to contrast with this permanent structure a form of stoma and sort of adjoining tissue which are a part of evanescent organs, and which also appear to have somewhat different functions. I have reference to the stomata of the leaves of *Opuntia versicolor*. The permanent stomata of this *Opuntia* closely resemble those of *Echinocactus* but the temporary stomata, those of the leaves, are very

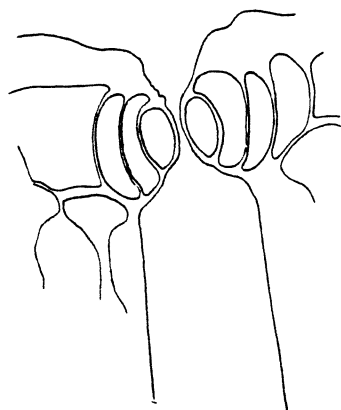


FIG. 9.—*Echinocactus wislizeni*. Stomata and substomal canal which passes through the supporting tissue (see Fig. 7) to the more deeply placed chlorenchyma (Fig. 6).

different (Figs. 12-14). These stomata are superficially placed

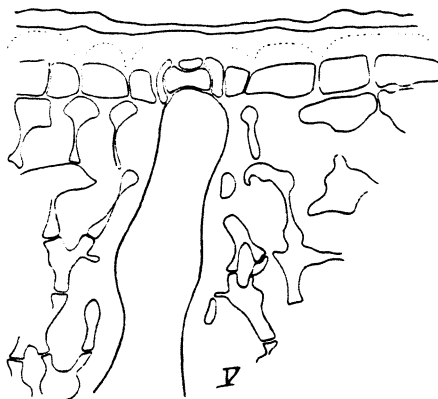


FIG. 10. — *Echinocactus wislizeni*. Same as Fig. 9, to show character of supporting tissue.

and they open directly into the substomal chamber (Fig. 12). The substomal canal of the permanent organ, therefore is lacking. Associated with this form of stoma is the absence of a sclerenchymatous supporting tissue, and, consequently, the extension of the chlorenchyma to the epidermis. The heavy outer epidermal wall of the older portions of *Echinocactus* is here replaced by a delicate one. In connection with this structure of the leaves of *Opuntia* appears their function of promoting transpiration, and presumably the respiratory activities as well, and in this they render it an important service, as will be apparent from the results of the transpiration studies.

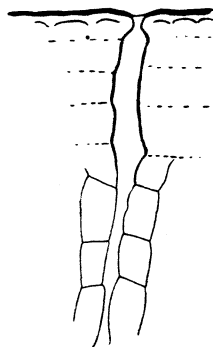


FIG. 11. — *Echinocactus wislizeni*. Semidiagrammatic sketch showing the relations of the substomal canal. That portion of it which is in the supporting tissue is heavily shaded; that portion in the chlorenchyma is represented by a lighter wall.

TRANSPIRATION OF CEREUS AND ECHINOCACTUS

In all of the studies on the transpiration of cacti which were conducted outdoors the polymer method (Cannon :05a), described elsewhere, was employed. A few, however, which will be pointed

out later, were done in the laboratory by weighing in a manner

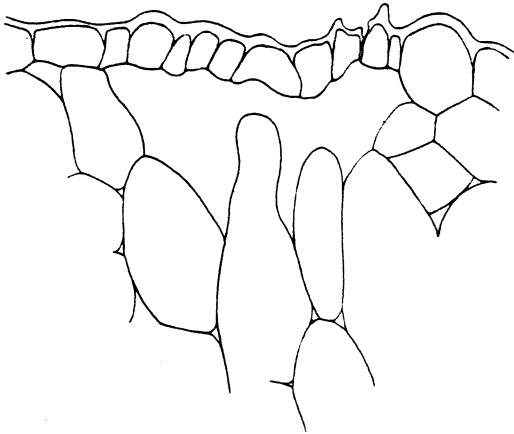


FIG. 12.—*Opuntia versicolor*. Cross section of a leaf showing two stomata, one of which was cut in two at right angles to the guard cells and the other parallel to and to one side of them. The confluent substomal chamber is shown. This section is to be contrasted with Fig. 13.

to be described. This change in method was made necessary on account of the high relative humidity prevailing at the time.

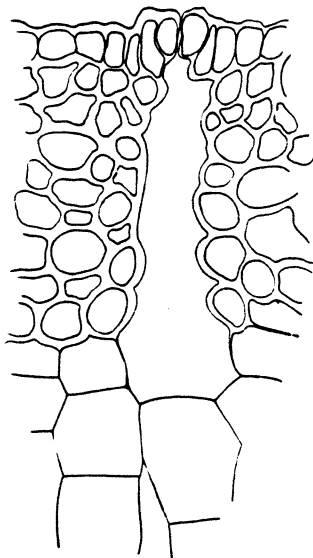


FIG. 13.—*Opuntia versicolor*. Substomal canal and partly developed supporting tissue of a young stem.

Experiment No. 1. Cereus giganteus

Time	Percent of Saturation	Temperature	Amount in Milligrams
9:27 A. M.	42.0	94° F.	67.5 ¹
10:37 A. M.	48.5	105° F.	106.0

The cactus was located in the shade of a *palo verde* (*Parkinsonia microphylla*) on a dry mountain-side not far above the bed of Salvino Canyon, 18 miles east of the Laboratory. Higher

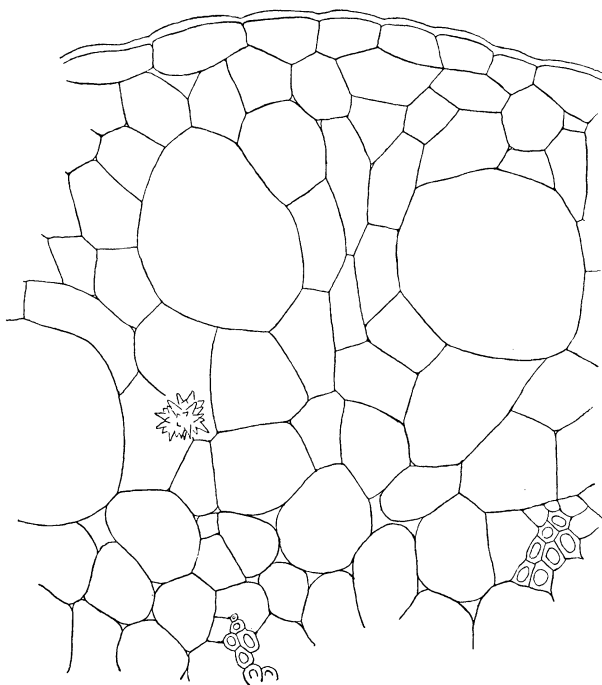


FIG. 14.—*Opuntia versicolor*. Cross section of a leaf to illustrate its delicate structure.

on the same slope were many other giant cacti of large size, and other typical desert plants such as *Encelia farinosa*, *Fouquieria splendens*, as well as other species of cacti.

¹ The first amount in each case is the absolute humidity of the atmosphere of the bell glass when the experiment begins. The second amount is the absolute humidity at the close of the experiment. The difference between the two is the amount transpired.

The transpiration of the cactus was taken September 9, and as the high relative humidity at the beginning of the experiment shows, the effects of the rains of August were still manifest. The rate which is 0.2 milligrams per minute for 100 sq. cm. of transpiring surface, may be considered a high one, since without exception the greatest rate of transpiration of all the plants, whose seasonal variation in rate has been observed, has been after or at the time of the summer rains.

Experiment 2. Echinocactus wislizeni

Time	Percent of Saturation	Temperature	Amount in Milligrams
10: 28 A. M.	32.5	82° F.	36.0
2: 05 P. M.	35.5	91° F.	51.0

This experiment took place on March 19, at the Desert Botanical Laboratory.

The rate of transpiration of the entire plant per hour is 3.4 milligrams.

On September 3 the experiment was repeated when the following data were derived:—

Experiment 3. Echinocactus wislizeni

Time	Percent of Saturation	Temperature	Amount in Milligrams
12: 24 P. M.	35	104° F.	60
3: 14 P. M.	45	109° F.	89

The rate for the entire plant is 9.6 milligrams per hour.

This specimen of *Echinocactus* is growing on a westerly slope on the Laboratory Mountain. In its vicinity are found a few giant cacti and *Encelia farinosa*, *Lycium* sp., and *Parkinsonia microphylla*. Because of the desirability of preserving this specimen the surface was not computed and therefore the rate cannot be compared directly with that of *Cereus giganteus* as given in the preceding experiment. However, it happened that the two cacti were of nearly the same size,—10 cm. in height,—and a general comparison between the two can be made. The rate of

Cereus per hour was approximately 33 milligrams while that of *Echinocactus* on September 3 was 9.6 milligrams. Whether this difference in the rate is constant for the two genera, or is attributable to other and unknown causes aside from the relatively slight difference in surface, is not known.

TRANSPIRATION OF *Opuntia versicolor*

A specimen of *Opuntia versicolor* about 20 cm. high, growing near the laboratory building, was studied at various times during the dry portions of the year (1904), namely, in March, April, June, and July. The observations indicate that the reaction of *Opuntia* to water is very different from that of other desert plants, such for instance as *Covillea tridentata*, *Encelia farinosa*, or *Fouquieria splendens* (Cannon, :05a, p. 404), suggesting a unique position among its associates and an important factor among the varied ones that brought about the present distribution of the group to which it belongs.

As has been shown in another place, the transpiration of *Fouquieria splendens*, as well as that of other desert plants and plants of more humid regions (Burgerstein, :04), under certain conditions increases with an addition to the available water supply (see Cannon, :05b; V. M. Spalding, :04, :05). Thus after rains, but before leaves appeared, the rate of transpiration of *Fouquieria splendens* increased about three fold; after leaves had been formed and while they were developing the rate was relatively very great. A similar condition was likewise observed in *Encelia farinosa*, *Covillea tridentata*, and in other plants. In *Opuntia versicolor*, however (see Figs. 2, 3), and probably in other *Opuntias* the response to the rains is indeed also positive but in a very different way. The cactus absorbs water greedily, and as a consequence it at once increases in size, and its tissues become turgid. But, so far as I observed, the rate of transpiration did not increase proportionally. Indeed, laboratory experiments, in which a small specimen of *O. versicolor* was attached to a potometer by a long delicate tube so that the cactus could be weighed at intervals at the same time that its rate of absorption was being recorded, showed very clearly that under such

conditions the cactus may absorb water much faster than it gives it up by transpiration.

It should be noted that the specimens of cactus which were experimented upon both in the field and in the laboratory did not have an adequate water supply at their disposal previous to the times of the experiments. As a general thing not until some time has passed after the water has been absorbed, does new growth appear with its embryonic structure and its evanescent leaves and then only does the rate of transpiration become greatly increased. During the periods of drought the plants make but little new tissue. These peculiarities of *Opuntia versicolor* were observed repeatedly and will be presented in the succeeding *résumé* of representative experiments.

The transpiration of *Opuntia versicolor*,—an entire plant,—was as follows:—

March 25	51.0	milligrams in one hour
March 26	63.0 ¹	" " " "
April 25	19.9	" " " "
June 30	27.5	" " " "
July 4	26.1	" " " "

During the period from March to July the rainfall was unusually small and the cactus had an insufficient supply of water. The rates of March, April, and June, therefore, represent the transpiratory activities of the plant in times of drought. At various times in the midst of the dry seasons Fouquieria, Covillea, and other plants had been irrigated and the effects on their transpiration were recorded (Cannon, :05b). To learn how an increase in the water supply of *Opuntia versicolor* would influence its rate, as well as to learn how the rate under such circumstances would compare with that during dry conditions, it, also, was irrigated. On June 27, which was a time of drought, nine gallons of water were poured slowly on the ground at the base of the cactus, but it did not show by an accelerated rate (see the rate of July 4, above) that it had absorbed any of the water. That it had really done so, however, was indicated by the fact that the plant had become rigid by the increased turgescence of its tissues.

¹ Unfortunately a small branch was broken from the plant after this experiment so that the winter and the summer rates are not comparable.

The transpiring surface of the *Opuntia* was not estimated, so that its rate cannot be compared directly with the rate of other cacti or plants of other families although this, perhaps, is of minor consequence. The important fact was established that the plant does transpire measurable amounts of water even in the driest times and that it absorbs water quite out of proportion to its rate of transpiration.

I wish now to call attention to a phase of the biology of *Opuntia versicolor* which is also of great importance in the economy of the plant but which has hitherto received little emphasis, namely, to the rôle which the leaves play in transpiration.

On August 18 the polymeter apparatus (Cannon, :05a, Fig. 4) was adjusted to take the transpiration of a branch of the cactus which bore leaves and which was situated a few meters north of the laboratory building. The data derived from this experiment are as follows:—

Experiment 4. Transpiration of Leaves of Opuntia versicolor

Time	Percent of Saturation	Temperature	Amount in Milligrams
2:20 P. M.	40	95° F.	62.
2:30 P. M.	59	98° F.	101.

The branch transpired at the rate of 234 milligrams in one hour, or 0.91 milligrams per minute for 100 sq. cm. of transpiring surface.

As soon as the experiment was finished the surface to the stem was coated with vaseline and the experiment was repeated. The following, therefore, is the transpiration of the leaves only.

Time	Percent of Saturation	Temperature	Amount in Milligrams
2:42 P. M.	41.5	97° F.	69.
2:52 P. M.	52.0	100° F.	87.

The rate per hour for the leaves of the branch is 108 milligrams, or 0.42 milligrams a minute for 100 sq. cm. of surface.

The surface of the stem alone was estimated at 331 sq. cm.; that of the leaves at 97 sq. cm. Therefore with somewhat less

than one fourth the entire transpiring surface, the leaves alone transpired nearly one half the whole amount.

The high humidity at this time was unfavorable to the further use of the polymeter method so that the experiments upon the transpiration of the leaves of the cactus were continued with a special weighing apparatus in its stead. Since the results of all of these experiments were essentially alike, I shall refer to one of them only.

A branch of *Opuntia versicolor* with leaves was placed in a bottle containing water which was so arranged, with a capillary tube as well as the branch fastened in the stopper, that the air could enter and maintain a pressure within uniform with that of the room, while only an inappreciable quantity of vapor escaped. In one hour, 2 : 15 to 3 : 15 P. M., the branch lost 180 milligrams in weight. The stem was then coated with vaseline and in one hour, 3 : 30 to 4 : 30 P. M., the loss of weight was 100 milligrams, which was, of course, the transpiration of the leaves only.

There were 69 leaves on the branch whose entire surface was estimated at 55 sq. cm. The surface of the stem alone was 65 sq. cm. Therefore the leaves had about 45 percent of the entire transpiring surface and they gave off about 55 percent of the entire amount transpired.

SUMMARY AND CONCLUSIONS

The leading points in this paper and the conclusions may be briefly stated in the following summary.

1. The root systems of *Cereus giganteus* and of *Echinocactus wislizeni* which were studied and mapped, present characteristic differences. The root system of *Cereus* is in part superficial and in part deeply placed. The root system of *Echinocactus* is superficial only. There appears to be a relation between the character of the root systems of these plants and that of the habitats in which they naturally occur. For example, the form and the extension of the roots of *Cereus* inhibit its occurrence in localities where the underlying formation is of such nature that they cannot reach the usual or needful depth. We accordingly find the plant on rocky mountains, or where the soil is deep, but in this locality

it does not grow at all, or rarely, on the *mesa* where the rock-like *caliche* forms a thick and nearly impenetrable stratum which reaches almost to the surface. However, it may not be wholly a problem of anchorage, since the morphological condition may be associated with a physiological one, as for instance, subirrigation or proper drainage which may be indispensable factors in its water relations. Although the character of the root system may thus be closely connected with the character of the habitat, certain features in the local distribution indicate that it cannot be too narrowly insisted upon. For example, *Cereus giganteus* avoids northern slopes, although to all outward appearances the structure and the water supply may be quite the same as on the other sides.

Echinocactus presents quite a different condition of affairs. The plant does not require unusual protection against lateral stresses. It grows most abundantly in this locality on the *mesa* where the soil is shallow. The roots are so placed that they can neither afford safe anchorage for a tall plant, nor absorb water at the water level. There is therefore a direct relation between the character of the plant and that of the root system, on the one hand, and the character of the root system and that of the habitat, on the other. It should also be noted that the roots of Echinocactus, which are very shallowly placed, permit the plant to derive benefit from relatively small rains, but, by the same token, that they prevent it from getting water other than what falls on the area included by them.

2. The striking disproportion between absorption and transpiration, which was observed in *Opuntia versicolor*, is thought to be of great importance in accounting for the distribution of the plant (and perhaps of the family) in those parts where evaporation greatly exceeds precipitation.

3. A low rate of transpiration was demonstrated in *Opuntia versicolor* and *Echinocactus wislizeni* during periods of prolonged drought. At the time of the summer rains the rate was greatly increased and in all instances the increase was associated with the renewal of growth.

4. A direct relation was observed between structure and transpiration. The mature portions of Echinocactus and of *Opuntia*

versicolor are suited by the heavy outer epidermal wall, which is cuticularized, as well as by the stomata of peculiar structure, to resist rapid loss of water. This is the type of structure that is to be found during the periods of drought. The embryonic portions of these cacti, and the evanescent organs, in which are included the leaves of *Opuntia*, are well adapted to promote transpiration. This is accomplished in the embryonic tissues by a thin epidermal wall and by the undifferentiated portions of the outer part of the cortex by which a rapid transfer of water is possible. The substomal tube functions also throughout its entire length as the substomal chamber. In the leaves of *Opuntia* not only is the epidermal wall delicate, but the outer cortex is never differentiated into sclerenchyma and chlorenchyma and there is no substomal canal. Such is the structure of the tissues at the times when the rate of transpiration is most active.

5. The leaves of *Opuntia versicolor* play an important rôle in transpiration. In one instance with somewhat less than one fourth the entire transpiring surface the leaves transpired nearly one half the whole amount. In another instance about 45 percent of the entire transpiring surface was foliar and the leaves transpired about 55 percent of the total amount.

DESERT BOTANICAL LABORATORY
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